

NEW FIELD OBSERVATIONS ON BURROWING IN EPHEMEROPTERA FROM AROUND THE WORLD¹

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ABSTRACT: New observations on burrowing behavior of mayfly larvae are given for the leptophlebiids *Paraleptophlebia packi* and *P. bicornuta* in North America, and *Jappa kutera* in Australia; for the potamanthids *Potamanthus idiocerus* in Taiwan, and *P. formosus* and *Rhoenmanthus speciosus* in Malaysia; for the polymitarcyids *Probosciodoplocia* spp. in Madagascar, *Afroplocia sampsoni* in South Africa, and *Ephoron album* in North America; and for the ephemerids *Ephemera simulans* and *Litobranchia recurvata* in North America, and *Palingenia fuliginosa* in east Europe. *Paraleptophlebia packi* forms burrows in silt, whereas *P. bicornuta* is an interstitial dweller. *Potamanthus idiocerus* and *R. speciosus* are the first species of Potamanthidae known to form burrows in silt; however, *P. formosus* is more typical of the family in that it is an interstitial dweller. Silt burrows made by Leptophlebiidae and Potamanthidae are formed along a rock interface and are never U-shaped, but those formed by advanced burrowers in the Polymitarcyidae and Ephemeridae are independent of rocks and often U-shaped. New evidence of burrowing in plesiotypic polymitarcyid lineages with flat-bodied larvae, represented by *Probosciodoplocia* and *Afroplocia*, is provided. *Ephoron album* is a highly flexible burrower; its larvae form burrows in depositional substrates, but are interstitial dwellers in erosional substrates. *Palingenia fuliginosa* is the first non-polymitarcyid burrower to be found burrowing in wood.

Many mayflies live within the substrate of bodies of freshwater during at least part of their larval life. Some inhabit interstitial areas of substrate temporarily as very young larvae (see e.g., Coleman and Hynes 1970, Williams 1984), evidently acquiring some protection in such habitats during this part of their lives, but otherwise showing no particular adaptations for subbenthic habitats. Although these mayflies may be associated with hyporheic nurseries as early instars, they are generally surface benthos. Some sprawler and clinger mayfly larvae are known to move vertically through the substrate on a daily basis (e.g., see Glozier and Culp 1989), and some of these may occur under the buried undersides of stones or other surface substrates especially during daylight hours. Many mayflies are associated with fine sand or sand/silt habitats, and are notable in lotic environments with shifting sand substrates. Those known as psammophilous mayflies typically show adaptations for living on, or partially to completely buried within, the sandy substrate (see e.g., McCafferty 1991b).

The above mentioned mayflies, although they may move into interstitial areas temporarily or may settle in fine substrates, have not traditionally been known as burrowing mayflies. The term burrowing, when applied to Ephemeroptera, has generally been applied to those mayflies that demonstrate adaptations for excavating and residing more-or-less permanently within substrates

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that include coarse sand, silt, sand/marl, clay, mixed gravel, wood, and fresh-water sponges.

Bae and McCafferty (1994) indicated that there were two main categories of burrowing mayflies, based on their ecology and behavior. Those that have been designated as interstitial dwellers by Bae and McCafferty (1995) actively burrow in interstices or available crevices, and although capable of excavating, they are limited in their ability to manufacture and maintain actual tunnels, or burrows, within the substrate. Burrowers in coarse sand and mixed gravel, such as *Dolania americana* Edmunds and Traver (e.g., see McCafferty 1975, Edmunds *et al.* 1976) and *Anthopotamus verticis* (Say) (see Bae and McCafferty 1994) generally fit the interstitial dweller category. Burrow dwellers (Bae and McCafferty 1995), on the other hand, construct and dwell within walled, sometimes U-shaped burrows in finer and more compacted materials or solid substrates. The most detailed study of such burrowers was provided by Keltner and McCafferty (1986) in their videomacroscopic study of *Hexagenia limbata* (Serville) and *Pentagenia vittigera* (Walsh).

Burrowing, as it is known in Ephemeroptera, is also associated with one particular evolutionary lineage of mayflies known as the infraorder Lanceolata (McCafferty 1991a). This grouping includes the superfamilies Leptophlebioidea, Behningioidea, and Ephemerioidea. Fossorial adaptations are most highly evolved in the Ephemerioidea.

Mandibular tusks are structural adaptations most commonly associated with burrowing mayfly larvae. Tusks are present in all ephemeroid mayfly larvae, and only in a few cases have become secondarily reduced (McCafferty and Edmunds 1973, McCafferty and Gillies 1979, Bae and McCafferty 1991). Burrowing is not widespread in the large superfamily Leptophlebioidea, but tusks are present in larvae of most of the few leptophlebioids that are known to burrow. Leptophlebioid mandibular tusks are not homologous with ephemeroid tusks (Needham *et al.* 1935). Mandibular tusks are entirely absent in the behningioid burrowers. Bae and McCafferty (1995) recently treated the origin of Ephemeroptera tusks and their radiation and structural adaptations in relation to the evolution of burrowing behavior and ecology.

Over 100 literature sources of published information on burrowing in mayflies was reviewed by Bae and McCafferty (1995). The purpose of this paper is to present new field observations on Ephemeroptera burrowing, and to draw pertinent comparisons with previously published data. Many of the new observations were made on foreign collecting expeditions, where time was limited and experimental facilities were not available.

***Paraleptophlebia* (Leptophlebioidea: Leptophlebiidae)**

Within the genus *Paraleptophlebia*, stream-dwelling larvae of four of the

western North American species have mandibular tusks. These tusks, however, are not derived from the body of the mandible as in Ephemeroidea, but rather from the incisors of the mandibles. The habitats of *P. bicornuta* (McDunnough) and *P. packi* (Needham) were treated somewhat by Lehmkuhl and Anderson (1971) and Needham (1927), respectively. We have new observations regarding the behavior of these species: The most abundant tusked *Paraleptophlebia* species, *P. bicornuta*, moves freely through interstices of gravel and cobble substrate. *Paraleptophlebia packi* in Utah, however, maintains long burrows, up to 40 cm in length, along the interface between large boulders and silt deposits. When boulders are disturbed, the burrows collapse, but the burrow tracks along the boulder often remain evident. Our observations thus indicate that both interstitial dwelling and a crude type of burrow dwelling exist in Leptophlebiidae with mandibular tusks. Nothing is known of the presumed burrowing habit of *P. helena* (Day) or *P. zayante* (Day) of California.

***Jappa* (Leptophlebioidea: Leptophlebiidae)**

Larvae of the eastern Australia genus *Jappa* are also known to burrow (see Peters and Campbell 1991, and review by Bae and McCafferty 1995). These larvae do not have mandibular tusks, but instead possess cephalic tusks (elongated frontal horns on the head). Bae and McCafferty (1995) regarded these as most analogous with the mandibular tusks of *Rhoenanthus* (Ephemeroidea: Potamanthidae). Larvae are known to burrow along mud/rock interfaces, and in gravel and sand. The new observation reported here is that in New England National Park N.S.W., larvae of *J. kutera* Harker burrow along rocks only ca 10-15 cm in diameter, the largest available for burrow interfacing. The habitat of these larvae was a large diffuse spring-saturated area having many rivulets and a mud substrate with moss and other low vegetation.

***Potamanthus* (Ephemeroidea: Potamanthidae)**

Bae and McCafferty (1991) indicated that all genera of the Potamanthidae had been confirmed to burrow (see also review of Bae and McCafferty 1995). A critical laboratory study of the eastern North American species *Anthopotamus verticis* by Bae and McCafferty (1994) clearly demonstrated the burrowing habit, and therefore substantiated anecdotal and incomplete field observations that had appeared up to that time. This, in part, also refuted the popular notion that potamanthid larvae were typical sprawling benthos because they had flattened bodies. We have made additional observations of burrowing in the family Potamanthidae.

Larvae of *P. (Potamanthodes) idiocerus* Bae and McCafferty were observed and collected in a silted river in Taiwan. Mature larvae were found in distinct, long burrows, ca 30 cm long. The burrows were at the interface of silt and

boulders. When boulders were moved the burrows collapsed, but the paths of the burrows on the boulders were evident. The larval microhabitat was similar to that of *Paraleptophlebia packi*, as reported above. Larvae of *P. (Potamanthodes) formosus* Eaton in Korea had been found to live interstitially by Bae (in Bae and McCafferty 1991); however, no details were provided at that time. Additional observations of this species were made from north of Kuala Lumpur, Malaysia. Larvae occurred in stream bottoms with a mix of rocks, gravel, and sand, where they occupied, perhaps exclusively, interstices in gravel beneath moderate to large boulders. Their habit and habitat is evidently similar, at least in part, to that detailed for *Anthopotamus* in North America by Bae and McCafferty (1994).

***Rhoenanthus* (Ephemeroidea: Potamanthidae)**

The only comprehensive study of burrowing in Potamanthidae (Bae and McCafferty 1994) indicated that the American genus *Anthopotamus* is an interstitial dweller. Observations of *Rhoenanthus speciosus* Eaton from Sabah indicate that mature and nearly mature larvae of this species burrow at the interface of silt and 10-15 cm diameter rocks. This observation, along with the observations of the larvae of *P. idiocerus* in Taiwan, reported above for the first time, indicate that structural burrows can be formed in silt along the interface of rocks by certain species of Potamanthidae. Technically, this would qualify them as burrow dwellers (*sensu* Bae and McCafferty 1994).

***Proboscidoplocia* (Ephemeroidea: Polymitarcyidae)**

Proboscidoplocia belongs to the subfamily Euthyplociinae, one of the primitive lineages of Polymitarcyidae (McCafferty 1991a) that has dorsoventrally flattened larvae. Very little information on the microhabitat of this subfamily has been available, except for some recent observations of *Euthyplocia hecuba* (Hagen) from Costa Rica. Sweeney *et al.* (1995) reported that larvae of *Euthyplocia* burrow under small to large cobbles embedded in stream beds with a sandy matrix. Given such substrate type and the fact that filtering setae occur in rows along the mandibular tusks in this genus (Bae and McCafferty 1995), we deduce that these larvae feed within the substrate, similar to that described for *Anthopotamus verticis* by McCafferty and Bae (1992). An additional observation from this subfamily is of *Proboscidoplocia* spp. from Madagascar, including *P. sikorai* (Vaysierre) and possibly undescribed species. Larvae were collected from the upper 15 cm of sand around the base of cobble. This suggests a habit and habitat somewhat similar to that of *E. hecuba* (see above). We do not know if any of these Euthyplociinae larvae form burrows along the rock interface.

Afroplocia (Ephemeroidea: Polymitarcyidae)

Another primitive subfamily of Polymitarcyidae is the Exeuthyplociinae (McCafferty 1991a), which consists of two African genera, *Afroplocia* and *Exeuthyplocia*. Although Gillies (1980) suggested that larvae of this group may indeed burrow, there have thus far been no actual observations of such. Adding to this distinct possibility is the new observation from the Mooi River in Natal, South Africa, where larvae of *Afroplocia sampsoni* (Barnard) were kicked from within mixed substrate ranging from silt/sand to small cobble. From this incidental data, we do not know whether *Afroplocia* larvae are interstitial dwellers or burrow dwellers utilizing rock interface, although the absence of pure silt may preclude burrow formation.

Ephoron (Ephemeroidea: Polymitarcyidae)

Bae and McCafferty (1995) reported that *Ephoron* larvae (subfamily Polymitarcyinae) form and maintain distinct burrows when the substrate is appropriate, but can be interstitial dwellers under other substrate conditions. New observations corroborate this flexible range of burrowing. In Utah, *E. album* (Say) larvae burrow in the clay banks and bottoms of the Jordan River and associated irrigation canals, and appear to form U-shaped burrows typical of many advanced burrowers. When the water level drops, the honeycombed banks are reminiscent of those of *Tortopus* (another polymitarcyid in the subfamily Campsurinae), as illustrated by Scott *et al.* (1959). In contrast, *E. album* larvae from the Green River, where cobbles are embedded in clay, burrow along the clay-rock interface and the burrow is apparently not U-shaped. In erosional areas of the Tippecanoe River in Indiana, *E. album* larvae have commonly been taken from mixed gravel and cobble substrate, where they exist as interstitial dwellers. In depositional areas of the Tippecanoe River, this same species forms burrows in silt and marl substrates. *Ephoron leukon* Williamson, a species that cohabits the Tippecanoe River with *E. album*, is only known from erosional areas where it is an interstitial dweller. Based on collecting data, *E. savignyi* (Pictet) in southern Africa may also be as flexible as *E. album* with respect to being an interstitial dweller or burrow dweller.

Ephemera (Ephemeroidea: Ephemeridae)

Among the subfamily Ephemerinae of the Ephemeridae, we have found *Ephemera simulans* Walker in a variety of habitats. The species occurs in a broad spectrum of streams and lakes throughout much of North America. In Crawford Creek and the Firehole River in Yellowstone National Park, larvae inhabit loose sand, including small sandy pockets in cavities of volcanic rock,

ca 2-3 cm in diameter. In the Uintah River in Utah, larvae occur near the stream margin in silt and sand mixture. This species cohabits the river with the burrowing ephemeropterid *Hexagenia limbata* (Serville), which forms burrows in silt and marl. In Indiana, *E. simulans* larvae occur mainly in erosional areas of streams with mixed sand and gravel substrates. The species is apparently an interstitial dweller, and our observations support those of Eriksen (1964), who demonstrated in laboratory studies that the species tended to select fine gravel. Although the larvae could burrow in a variety of substrate types, the relatively low DO of finer sediments, such as silt, limited this species to substrates with larger interstices (Eriksen 1968). *Ephemera danica* Müller in Europe is known to occur in sand and gravel as young larvae and in gravel as mature larvae (Tolkamp and Both 1978). *Ephemera vulgata* L., in contrast, is known to be a burrow dweller (e.g., Verrier 1956), often in clay substrates.

***Litobrancha* (Ephemeroidea: Ephemeridae)**

The eastern North American burrowing mayfly *Litobrancha recurvata* (Morgan) is a member of the subfamily Hexageniinae, all members of which are known to be burrow dwellers with advanced burrowing behavior (Bae and McCafferty 1995). Classic respiratory studies by Morgan and Grierson (1932) and Morgan and Wilder (1936) were performed on *L. recurvata* from small sand bottomed streams in Massachusetts. New observations of *L. recurvata* larvae from streams in the upper peninsula of Michigan clearly show them to be U-shaped burrow dwellers in heavy, organically rich silt. Given the fact that *Litobrancha* larvae have similar structural adaptations to those of the closely related *Hexagenia* (see Keltner and McCafferty 1986), there can be little doubt that the larvae studied by Morgan and her coworkers were also taken from silt deposits.

***Palingenia* (Ephemeroidea: Ephemeridae)**

Palingenia is a member of the subfamily Palingeniinae of the Ephemeridae. Its members, like those of the Hexageniinae and Pentageniinae, are known to be burrow dwellers exclusively (see Bae and McCafferty 1995). Along with the Pentageniinae, the Palingeniinae is considered the most apotypic lineage in the family (McCafferty 1991a). *Palingenia fuliginosa* (Georgi) is a European species known to burrow in river silt (e.g., Soldán 1978). While collecting in Slovakia, a decayed log of driftwood about 10 cm in diameter was broken open to reveal a larva of this species. Although wood burrowing, even in teak and bamboo, is well documented in the subfamily Asthenopodinae (family Polymitarcyidae) in the Orient, Africa, and South America (e.g., Vejrabhongse 1937, Hartland-Rowe 1953, Sattler 1967), this is a new and unexpected observation for the family Ephemeridae.

EVOLUTIONARY IMPLICATIONS

Silt burrows in Potamanthidae and Leptophlebiidae evidently require a rock interface, and they do not appear to be as structurally advanced as the uniformly walled and often U-shaped burrows constructed by the more advanced burrow dwellers in the apotypic lineages of Polymitarcyidae and Ephemeridae (see Bae and McCafferty 1995). Based on phylogenetic relationships (McCafferty 1991a, Bae and McCafferty 1995), interstitial dwelling, which may or may not require a rock interface, may be deduced to be the most primitive type of burrowing. Some close relatives of interstitial dwellers can form burrows. These burrow dwelling larvae apparently require a rock interface for mobility and purchase by the larvae, because they do not have adaptations for moving in silt as are present on the legs of the more advanced burrow dwellers (see Keltner and McCafferty 1986). Such adaptations include, for example, large spurs, expanded tibiae, and developed tibial processes. Primitive burrows formed along rock surfaces represent a likely step in the evolution from interstitial dwelling to burrow dwelling independent of rock surfaces, at least in the Potamanthidae-Ephemeridae lineage.

The more advanced type of burrowing and burrow formation developed independently in the Polymitarcyidae lineage and the Potamanthidae-Ephemeridae lineage, as detailed by Bae and McCafferty (1995). This dichotomy is evidenced by functional similarities, but adaptive structural differences, in the two lineages. The flat bodied burrowers in the plesiotypic subfamilies Euthyplociinae and Exeuthyplociinae of the Polymitarcyidae, just as the flat-bodied potamanthid larvae of the Potamanthidae-Ephemeridae lineage, are evidently interstitial dwellers or primitive burrow dwellers. Observations of Euthyplociinae larvae, at least, indicate that a rock interface is used in burrowing, but the observations of sand or sand matrix leaves some doubt as to whether an actual burrow can be maintained, depending on the quality of silt present. Nevertheless, we would not be surprised to find both interstitial dwelling and primitive burrow dwelling, which requires a rock interface, in these groups. An advanced type of burrow dwelling, independent of a rock surface, would seem to be out of the question for these groups because their larvae, like those of the Potamanthidae, demonstrate no adaptations for moving in silt. At least one species of more advanced Polymitarcyidae (see *E. album*, above) demonstrates all evolutionary gradations of burrowing habitat and burrow formation. As deduced for the Potamanthidae-Ephemeridae lineage, burrow dwelling along a rock interface also could have been the intermediate step in the evolution of more advanced burrowing in the polymitarcyid lineage.

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